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VEGETATION AS A DETERMINANT IN AVIAN ECOLOGY[1]

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Abstract: Vegetation, primarily by virtue of its structure, provides the setting in which most birds act out their ecological and evolutionary roles. Vegetation structure in both the vertical and horizontal dimensions affects avian community structure, but the horizontal component has received less attention from ecologists. Three heterogeneity indices, developed to quantify horizontal heterogeneity of vegetation, have received limited testing in Delaware, Illinois, and Texas. The indices resolve some problems in predicting community diversity, but their universality and applicability are still untested. At the individual and population level, vegetation can be a proximate or an ultimate factor of habitat selection, and can affect exploitation patterns of individual species. Habitat, nesting, and feeding data for several species in south Texas brush-grasslands demonstrate these points. The results suggest several points at both levels which need the attention of applied and non-applied avian ecologists working with both game and non-game birds.

"The world is a patchwork quilt," one of my principles of ecology, refers to the environmental mosaic created on the landscape by myriad combinations of overlapping gradients of environmental factors such as soil type, pH, insolation, moisture, and mineral content. These, in turn, affect patchiness of another environmental component—vegetation.

Vegetation adds dimension and variety to the landscape and provides the kind of environmental patchiness which is most apparent to us. It provides the framework—the setting or the limits—within which terrestrial, and many aquatic, birds olve and act out their ecological roles. Vegetation exerts this effect directly and indirectly through its structure and, in some cases, through special products such as fruits. It is common knowledge that vegetation is important to birds because it provides a variety of requisites: nest sites, song posts, food (directly in fruits and seeds and indirectly in invertebrates on the plants), and protection from predators and extreme weather. However, there are other ways in which vegetation influences avian ecology. Three of these relate to effects at the population level, and a fourth at the community level: (1) As a proximate factor, it can provide cues for habitat selection; (2) Vegetation can modify the ways birds exploit resources; (3) As an ultimate factor, it can affect the success of individuals and hence, populations in a particular habitat; (4) Finally, its complexity allows birds to subdivide resources such as food and space into patches, substrates, or strata. Because vegetation can play a major part in determining various community characteristics, it is a critical factor in much of avian ecology.

The above points have been discussed variously in several reviews of avian habitat research (Hilden 1965, Orians 1971, Balda 1975, Verner 1975, and Karr 1978). Therefore, I intend only to re-emphasize some key ideas about the relationships between birds and vegetation. I will concentrate on results from my south Texas work and from studies inspired by that work.

PATTERNS AT THE COMMUNITY LEVEL.

Spatial heterogeneity has been a watchword of attempts to explain why habitats hold the number of species they do. Much effort has been expended to quantify heterogeneity and to relate it to diversity of birds and other animals. The vertical profile measures such as foliage height diversity (FHD) and percent vegetation cover (PCVC) have yielded general correlations with bird species diversity (BSD) measured by the Shannon-Wiener information-theoretic equation from a variety of habitats (Karr and Roth 1971). These measures also have failed in numerous places (Roth 1976), perhaps partly because of a failure to account for other variables (Karr 1976, 1978). However, I contend that much of the scatter was because of inadequate indexing of spatial heterogeneity.

This inadequacy became apparent to me in a study of four plant communities in the south Texas brush-grasslands where BSD, FHD, and PCVC were fairly similar (Karr and Roth 1971). The indices could not predict the diversities of the four areas when treated as a distinct group. I believe this was because FHD and PCVC are functions of the proportion of vegetation in different layers, and not of the horizontal distribution of the vegetation in those layers. Hence, these measures may detect 70% cover in a layer, but they do not detect whether that 70% represents cover evenly dispersed over the area or clumped in one or a few places. Neither do they tell us about the variety of combinations of layers present. These deficiencies indicate a need for an index that incorporates the horizontal component of heterogeneity and predicts BSD, species richness, and other attributes of avian communities. The ideal index should be universally applicable,

easy to calculate, and require easily generated data. A critical criterion of the index is that it make ecological sense. If the index meets that need and also predicts community features, it should point to the factors which are important determinants of avian community structure.

Only Wiens (1973a, 1974), Blondel et al. (1973), and Roth (1976) have reported attempts at quantifying horizontal heterogeneity and relating it to avian diversity, although MacArthur et al. (1962) suggested it is of major importance. Pianka (1966) and Murdoch et al. (1972) attempted such correlations with lizards and insects. The remainder of this section will discuss three indices which I have developed and tested.

The first index has been described elsewhere (Roth 1976). It received its impetus from the Texas brush-grasslands where the varying density and dispersion of shrubs may be largely responsible for the variation in avian diversity among the four otherwise similar sites. A shift away from regular dispersion of shrubs should create patches of various densities. A greater variety of birds could distinguish and partition those patches than could do so in a uniform habitat (regular distribution) where patches were absent. The coefficient of variation of the point-to-plant distances from the point-quarter sampling method (Cottam and Curtis 1956) was used as an index (D) of this heterogeneity. D increased as dispersion went from regular to random (Roth 1976). Using distances to shrubs, D was significantly correlated with BSD for the four Texas areas, two Illinois shrubby areas, and four Delaware forests. Non-forests fit the line more closely than forests, and the relationship did not hold for D derived from point-to-tree distances for reasons explained elsewhere (Roth 1976). Despite the correlation, D lacked universal-
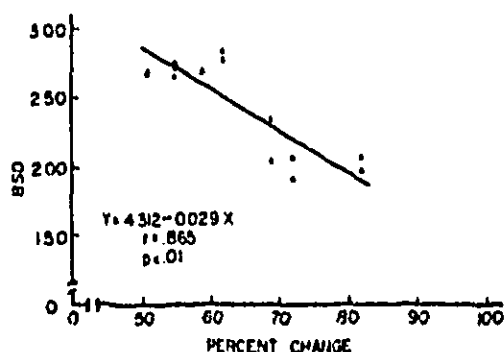
Figure 1. The relationship between bird species diversity (BSD) and percent change (see text) for eight Delaware woodlands in 1972 and 1973. Bird population data are from Martin (1976).

ity for two reasons: (1) absence of a plant life form, such as shrubs, common to all habitats and (2) the difficulty of application of the point-quarter method in various systems, for example, grasslands.

A more universal index would use a feature measurable in all habitats. The last two indices use such a feature—horizontal variation in vertical profiles. The biological rationale for the indices is my assumption that avian territories are three-dimensional, and that habitats are selected on that basis.

The first of these indices uses the combination of layers at a sample point as the data unit called *profile type*. In a one-layered habitat there are only two profile types: vegetation present or absent. With three layers, eight types are possible. This illustrates how additional layers of vegetation can increase habitat patchiness horizontally (MacArthur et al. 1962, MacArthur 1964, Roth 1976). Pearson (1975) also recognized "column-types" as important habitat features, but did not combine them into one index. Peter Martir and I indexed this characteristic by establishing evenly distributed transects in eight *Delaware* forest and parkland

sites. Presence or absence of vegetation was then determined in three layers (0–0.6 m, >0.6–6.0 m, >6.0 m) above hundreds of sample points 7.6 m apart along the transects. From that data set, we randomly selected many (equal to ca. 15% of the sample points) non-overlapping transects from six adjacent sample points enclosing five intervals, identified the profile type at each point, and determined the number of times that adjacent points had different profiles. This value was averaged over all transects. The procedure was repeated with two more sets of random transects (Table 1). The mean of the samples expressed as a percent is the index—percent change (PCHG). This index should distinguish habitats where similar profile types are clumped from ones where they are interspersed. It also should be sensitive to the variety of profile types in an area. Higher PCHG means greater heterogeneity and, one would predict, higher BSD. The correlation between PCHG and BSD was significant, but, surprisingly, negative (Figure 1). This is ecologically absurd, of course, because it predicts the highest BSD in the least heterogeneous area. One explanation for this apparent anomaly is that the relationship is curvilinear rather than linear, and that the curve will level off or perhaps decline somewhat at lower PCHG's; however, even a uniform habitat would support a few birds. At the upper end of the curve diversity should decline because extremely patchy habitats will have few blocks of preferred form (profile, gestalt) large enough to accommodate territorial activity and resource demands for many species. A curvilinear pattern would indicate that BSD is maximum at some intermediate patchiness.

It is relatively easy to collect the data for this index. Calculation of the index

Table 1. Sampling details and results used in calculation of percent change for eight Delaware woodlands.

Study area	Area (ha)	No. of transects	No. of changes of profile type/N intervals			
			Sample 1	Sample 2	Sample 3	Mean
Univ. Del. woods	14.5	158	2.8	2.7	2.9	2.8
Banning Park	9.2	132	2.6	2.6	2.6	2.6
Rittenhouse Park	4.4	102	2.9	2.6	2.7	2.7
Heritage Park	6.0	91	3.1	3.0	3.2	3.1
Windy Hills II forest	2.0	20	2.9	3.0	3.0	3.0
Windy Hills II strip	0.8	20	4.0	3.9	4.3	4.1
Windy Hills I	4.0	56	3.5	3.5	3.4	3.5
Pike Creek Park	2.3	42	3.5	3.6	3.6	3.6

was simple although generating the values was laborious. A computerized system of randomly selecting transects and determining the number of changes would speed up the process, and elimination or reduction of the non-overlapping transect requirement would simplify it. Random starting points are necessary to avoid the biases of starting repeatedly at the edge of an area and of repeatedly encountering recurring vegetation patterns. Random selection of the transects in the field during sampling would eliminate the excessive, unused points sampled by our scheme. The principal ecological weakness to the index is its use of a linear sample area which does not reflect the polygonal area which a bird uses. Some may object to the use of the three layers as arbitrary. They were used because of the success with their use in previous heterogeneity work (MacArthur and MacArthur 1961, Karr and Roth 1971). J. R. Karr (pers. comm.) has suggested that the distance between sampling points can affect this index. That possibility was confirmed by a test in which PCHG was calculated serially for intervals incremented by 1.5 m from 1.5 to 7.5 m (Martin 1976). Values generally increased through the series although in several cases no change or a reverse in the trend occurred between subsequent sizes. The

variation itself may reflect spatial patterns. Indices for areas which were obviously more uniform changed less than ones which were clearly more heterogeneous. Sampling interval may affect other indices also. Martin (1976) also found variation in PCVC (Karr 1968, Karr and Roth 1971) values in the same test, but FHD values were very consistent.

The third index has been tested only with Texas data. Intersections of a pre-existing 53 m grid system on each area determined the location of vegetation samples. About 35 sample plots on each area were centered on the grid intersections. Within each plot I recorded presence or absence of vegetation at 0, 0.15, 0.3, 0.6, 0.9 m, etc. upward through the vegetation at 13 sample points. One point was located at the grid intersection, and three lay along each of the four grid lines at 7.6 m intervals. A plot encompassed about 0.16 ha. I calculated percent cover at each height to generate a cover profile for each plot, averaged the profiles from all plots, and calculated the coefficient of variation (V) for each height i. The index, profile variation (PV), was then calculated as

$$PV = \sum_{i=1}^{n} V_i/L,$$
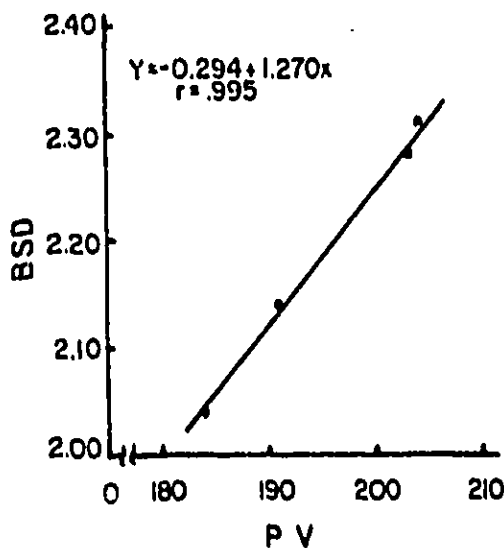
where n was the maximum number of

Figure 2. The relationship between bird species diversity (BSD) and profile variation (PV) for four Texas brush-grasslands. The slope differs significantly from zero ($F_{1,3} = .227$, $P < .01$).

heights with vegetation present on the study area, and L was the maximum number of heights with vegetation encountered among any of the study areas used in the analysis. Dividing by L rather than n standardized the index by compensating for the loss of all variation at upper heights on some areas because of absence of vegetation. A higher PV is assumed to indicate a patchier environment and should support a more diverse avifauna. Indeed, linear correlations with BSD were significant (Figure 2). Although this test is limited in terms of sample size and range of the index used, it suggests this approach deserves further evaluation.

PV indexes the horizontal variability of vegetation cover at each height so it has the advantage of combining vertical and horizontal patchiness. In addition it incorporates average cover values from patches of habitat (plots) resembling

usage areas of birds more closely than linear transects or random points. Additional data also may demonstrate the curvilinear relationship suggested with PCHG. Extension of testing to other habitats will require use of height intervals or layers more easily sampled than the 0.3 m ones, which would not be realistic in habitats with trees. Another problem is the need to recalculate the index in later analyses if the value of L changes because of inclusion of additional areas. The index requires data which may be more burdensome to collect and calculate, but it can be used in areas lacking arborescent vegetation. Of course, its between-habitat application remains to be tested also. Wiens (1974) used the coefficient of variation in a somewhat similar approach in grasslands but used total hits of vegetation above a point as his input. He found few relationships between the index and avian community structure.

These indices attempt to quantify an important determinant of avian community organization. Several areas of research are appropriate for the future. Tests of the indices in a wide variety of localities and habitat types are needed to determine universality. Indices should be rated on the basis of ease of data collection and ease of calculation of the indices. It should be determined if the indices are correlated with community characteristics other than the information-theoretic diversity index, especially when the latter is based on species. Some possible correlates include guild diversity, existence energy, and biomass. The usefulness and ecological meaning of the information index has been questioned (Hurlbert 1971, Karr 1976, 1978) as has the reliance on the species and on population density as ecologically meaningful units (Root 1967, Karr 1976, Roth 1977). Correlations between some of

these characteristics and various vegetation indices have been attempted (Karr and Roth 1971, Karr 1968, Wiens 1974).

Vegetation structure is not the only regulator of avian communities although, I contend, as did Wiens (1974) and Karr (1978), that it is a major factor. When a rapid index for predicting or estimating "carrying capacity" or evaluating habitat quality for birds is needed, vegetation structure should be the characteristic indexed. If other factors such as distance to colonization sources (MacClintock et al. 1977), shape and size of area (Galli et al. 1976, MacClintock et al. 1977, Diamond 1975), unique resources (Karr 1971, 1975), and history (Pearson 1975) can be incorporated with ease and efficiency, and can be justified by significantly improved predictability, they should be included. Such precision may not be needed in applied work, however.

PATTERNS AT THE POPULATION LEVEL

If vegetation is a determinant of community organization, it follows that it should be a determinant in the ecology of individual species that comprise the community. That vegetation is important as a proximate factor of habitat selection (Hilden 1965, Verner 1975) is suggested by our ability to associate species with certain habitat characteristics (James 1971). Some of these characteristics are apparent and can be stated subjectively. Others may be more subtle, but all should be quantifiable. Beyond that we also should be able to determine how vegetation affects birds in terms of their feeding styles, nest placement, survival, and ultimately, their reproductive success. In Texas I found evidence or examples of some of these relationships.

The study areas, chosen for their sim-

ilarity to one another, have been described (Roth 1976, 1977). They were 80–95 km apart and were located near Seadrift (Calhoun Co.), at the Welder Refuge (San Patricio Co.), south of Kingsville (Kleberg Co.), and north of Raymondville (Willacy Co.). I sampled vegetation in a way which enabled me to associate sets of sample points with approximate seasonal usage areas ("territories"; occupied sites) or with sites unused by a particular bird species. The usage areas were determined from seasonal composite maps compiled from spot-map censuses. Various vegetation characteristics were calculated for individual usage areas. Values for individual usage areas were weighted according to the number of sample points falling within the territory. All values for areas of a given species were then averaged together. These were compared with those from all unoccupied points which were grouped as a set. Wiens (1969) and Cody (1968) used a similar approach. I also recorded characteristics of feeding sites, behavior, and nest sites to determine how the various species used the vegetation. Roth (1971, 1977) detailed the procedures of vegetation sampling, avian censusing, and observations of feeding and nesting.

It was quite easy to understand the abundance and habitat preference patterns of some species without quantitative data. Common nighthawks (*Chordeiles minor*) occurred only at Seadrift (5 ♂♂/40 ha) because the very short, sparse ground cover (20% bare ground), typical of nesting sites of the species Dent 1940) was unique to that study area. The same cover, in company with shrubs, made Seadrift attractive to ground-foraging roadrunners (*Geococcyx californianus*) (5 ♂♂/40 ha) (Oberholser and Kincaid 1974:437). At the Welder Refuge the only sites lacking tall, herbaceous

Table 2. Some characteristics of vegetation in areas occupied and unoccupied by dickcissels at the Welder Refuge. Numbers in parentheses are number of sample points or number of shrubs used in the calculations.

Vegetation feature	Height (m)	Occupied sites	Unoccupied sites
Profile:		(291)	(331)
% cover	0.90	11.2*	4.5
	0.60	42.9*	32.0
	0.30	83.3*	76.9
	0.15	99.3	97.9
Shrub features:		(268)	(258)
Height ± S.E. (m)	—	2.2 ± 0.03**	2.4 ± 0.04
Volume ± S.E. (m³)	—	9.6 ± 0.90**	15.0 ± 1.51

* Significant ($P < .05$) O-U differences by t-test for equality of percentages (Sokal and Rohlf 1969 (a?))
** Significance O-U differences by t-test ($P < .05$).

cover were along mowed pipeline and power line rights-of-way that bordered the area, thereby restricting roadrunners to only a small part of the area. Short-grass sites were available at Kingsville, so the absence of roadrunners there must have another explanation such as a general southward, regional decline in abundance. While it was easy to identify qualitatively the breeding habitat preference for these two species, I could not identify unambiguously the specific factors on which individuals were cueing (proximate factors). Neither could I clarify factors that determined success nor the birds' exploitation patterns in the habitats.

It was possible, however, to quantify a subjective feeling about habitat preferences and the proximate factors of habitat selection for dickcissels (*Spiza americana*) and, in a limited way, to relate the vegetation characteristics to exploitation patterns and success. Dickcissels reportedly nest in south Texas in wet years when the grass is lush, but pass by in dry years without nesting (Clarence Cottam pers. comm., Oberholser and Kincaid 1974:870). Two consecutive years of high April rainfall (W. C. Glazener unpubl. data) resulted in a lush herbaceous growth on the Welder Refuge when the

birds arrived there in late April 1969. Nesting activities rapidly commenced about May 1. That the birds were responding to the tallgrass was evident in their presence only at the Welder Refuge (48 ♂♂/40 ha), in the vegetational characteristics of their territories vs. unoccupied sites, and in the temporal aspects of their presence.

A preference for dense herbaceous cover was indicated by greater cover at and below 0.9 m in territories as compared to unoccupied sites (Table 2). A significantly lower mean shrub height and volume in territories than in unoccupied sites (Table 2) suggested an additional preference for openness. In this case openness was a function of smaller shrubs, not of less dense shrubs, since densities did not differ.

The 10 nests found were 15–25 cm from the ground. Each was invariably associated with a small woody plant surrounded to a distance of at least 0.6 m by dense grass or forbs 0.6–0.9 m tall. The critical information on fledgling production was incomplete (two nests failed, two fledged young, and six unknown), so the role of vegetation as an ultimate factor could not be determined. However, Zimmerman (1971) demonstrated that male dickcissels in Kansas with territo-

ries having lush, tall growth, tended to attract more females and therefore rear more young than those in shorter cover. He sugg   ed the vegetation offered protection   i moderated the nest micro-climate. Pieszczynska (1978) showed the latter to be the advantage to lark buntings (*Calamospiza melanocorys*) nesting in tall grass, and, as with dickcissels, males with lusher territories were more likely to be polygamous. My censuses were not detailed sufficiently to detect polygamy.

A negative indication of the attractiveness of the lush vegetation occurred in May and June when rainfall totals were 11 and 23 cm less than in 1968, and the vegetation began to wither. As nests failed or young fledged, the birds left the area until only two pairs feeding fledglings remained on 16 June. None were seen after that date. It has been suggested that dickcissels stop in Texas and rear or attempt to rear a brood before moving to the central plains to breed again (Clarence Cottam pers. comm., Fretwell 1972). It is of interest whether this represents past selection on a northern population to breed earlier or to raise an extra brood, or selection on a southern population to compensate for unpredictable weather and vegetation conditions by moving north when conditions become poor. The latter would be suggested if birds spent the entire summer in south Texas in very wet years. Oberholser and Kincaid (1974:870) imply their presence in Texas in wet summers, but not specifically in south Texas.

Habitat preferences also are indicated when certain features are common to territories in different localities or sites. The cover profiles of ground doves (*Columbina passerina*) suggested this at Kingsville and Raymondville where territories had less cover and more cover, respectively, than unoccupied sites in the 1.2–
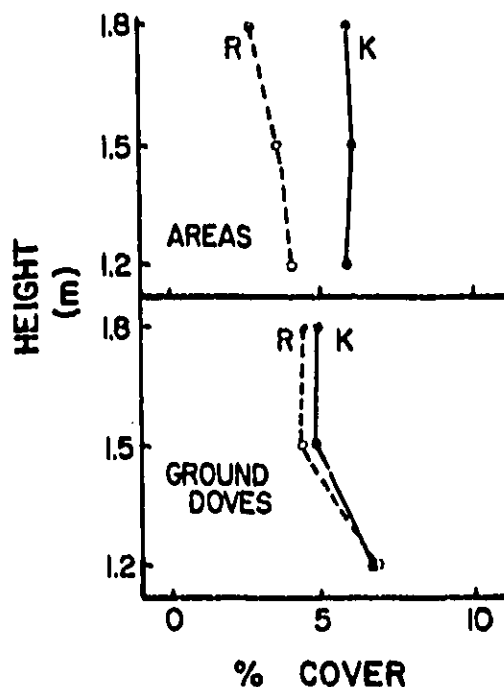

Figure 3. Vegetation cover profiles for the entire Kingsville (K) and Raymondville (R) study areas and for sites occupied by ground doves on the two areas. Number of sample points used for each profile were 658, 633, 61 and 118, respectively.

1.8 m height zone. However, resultant occupied cover values on the two areas were very similar, while the profiles of the entire study sites were considerably different ($P < .05$, t-test for equality of percentages at 1.5 and 1.8 m) (Figure 3).

These results suggest that the 1.5–1.8 m zone was important to habitat selection and presumably to some critical activity. Nest placement is suggested since ground doves usually feed on the ground. Indeed, at Raymondville 76% of 25 nests were 1.2–1.8 m above ground, and at Kingsville two of three were in that zone. The respective mean nest heights were 1.6 ± 0.06 (SE) and 1.3 ± 0.35 m (1.6 ± 0.07 for shrub sites, $N = 2$). No distinction in success between nests in and out

Table 3. Use of substrates by Bewick's wrens at three Texas study areas. The foraging pattern at Seadrift differed significantly from that at Kingsville. ($\chi^2 = 27.53$, $P < .001$). Welder Refuge data were not tested (see text). Chi square was calculated from the raw data.

Feeding substrate	Percent of observations		
	Seadrift (N = 56)	Welder (N = 19)	Kingsville (N = 34)
Ground-herb	41	11	31
Shrub foliage	7	5	33
Shrub bark	52	84	35

of the zone could be found. The much greater population at Raymondville (6 vs. 25 ♂ ♂/40 ha) more likely reflects a general regional increase southward than a scarcity of preferred sites at Kingsville. However, my data cannot exclude the latter possibility as an added cause of the population difference.

Foraging patterns of a species also can be affected by vegetative configuration. For example, Bewick's wrens (*Thryomanes bewickii*) were present at Seadrift, the Welder Refuge, and Kingsville in equal abundance (5, 5, and 6 ♂ ♂/40 ha, respectively). However, use of feeding substrates differed considerably among areas (Table 3), although shrubs had an effect on foraging in all cases.

Use of ground-herb sites at the Welder Refuge probably was underestimated because of occasional difficulty in seeing under "chaparral" clumps. While feeding, wrens often ceased calling for brief periods, a behavior observed in other places to be associated with dropping to the ground to feed. Because of this problem and the limited data, I will not comment further on the Welder Refuge wrens.

Ground or herb substrates often were used at Seadrift because many of the shrubs there had branches and foliage near or on the ground. The effect was a foliage-covered dome over a core of bare limbs with a shaded expanse of leaf litter, bare ground, and lichen-covered bark and seedlings beneath. While foraging on bark, wrens often came close to the ground and made brief forays to the ground to forage. Miller (1941) also noted this behavior.

At Kingsville the shift away from the use of ground-herb and, perhaps, from bark to shrub foliage was also a function of structure. Only two shrub species served as feeding sites there—huisache (*Acacia farnesiana*) and granjeno (*Celtis pallida*). Both were less abundant at Seadrift and the Welder Refuge. Huisache has loose, flaky bark on the trunk. It also was infested with a cerambycid beetle (*Oncideres* sp.). The beetle's girdling action caused many limbs to be partially or completely broken off and decaying wood to be exposed. Such features should have offered attractive sites for bark foraging. However, the growth form of huisache—usually of a cone or floral spray shape—left those sites exposed since foliage was limited to the upper parts of the shrub. Such exposure deters wren foraging (Miller 1941). The smooth bark of granjeno was used only incidentally as a foraging substrate. Mesquite (*Prosopis glandulosa*) also was present at Kingsville, but the limbs were above ground, and the lower branches were more exposed than at Seadrift. With the availability of secluded bark sites reduced, the birds shifted to foliage feeding.

Sixteen of 18 instances of foliage feeding were on granjeno. Its relatively large, simple leaves on short petioles are scattered throughout the height of the plant. They presumably would provide more cover and harbor more arthropods in accessible, but cryptic, places than hui-

sache or mesquite. Huisache has a sparse foliage of compound leaves with small leaflets in the upper parts of the shrub. Mesquite has larger compound leaves and leaflets, but they droop from long petioles and would be difficult to exploit except by hovering—an unknown technique for wrens.

One might conclude that these necessary shifts in foraging tactics had no effect on the success of the birds since the populations were equal on the three areas. However, I do not know what the relative regional populations for the three localities were. Perhaps the foraging strategies caused a reduction in one of the areas by reducing energy returns or reproductive success, but my data did not permit that evaluation. A more intensive study would be necessary to confirm this.

Another example of foraging shifts made necessary by vegetation structure also indicated effects on reproductive success and, in turn, on the evolution of habitat selection. In a comparison of foraging at Seadrift and the Welder Refuge 1 (Roth 1979) found that mockingbirds (*Mimus polyglottis*) responded very positively to the short grass of Seadrift (55 ♂♂/40 ha) because it favored the preferred feeding style—watching and running after prey from ground perches. On the other hand, at the Welder Refuge the tallgrass interfered with that foraging style and forced the birds to forage in the air or in shrubs, or to drop to the ground to seize prey sighted from shrub perches. The result was a lower population (13 ♂♂/40 ha) and abandonment of the area as the grass grew taller during spring. At Seadrift renesting persisted throughout the summer, presumably because foraging was more efficient or rewarding there. The net result was that the birds

eventually produced young while the Welder Refuge birds did not.

Three points should be made in summarizing this section. First, these cases demonstrate that vegetation does influence the ecology of individuals, and consequently, of populations. This is not startling news, but it is useful to be reminded of the subtle effects that small variations in vegetation can have.

Second, the results suggest that some exploitation patterns may be dictated simply by what is available for exploitation rather than by competition within that community. They also suggest that foraging patterns vary with vegetation structure just as they do with time of day, season, weather, and nesting stage (Root 1967, Grubb 1975, 1977, Salt and Willard 1971).

Third, a comment on the technique of comparing occupied and unoccupied sites is in order. This is one way of identifying factors which actually are associated with a territory, nest site, etc., and which may be proximate factors. It also may point to what is being avoided. However, there are some limitations. If a species prefers moderate cover, the unoccupied values may not differ if they are an average of the two extremes. Another source of ambiguity is suggested by results of Wiens (1973b) who found that habitat preferences of some species converged as the breeding season progressed, habitats became more crowded, and preferred areas were filled. Those findings suggest that if one waits until late in the season to sample the vegetation, the resultant species values could represent two classes of territories: ones settled early in preferred sites and ones settled later in the season in peripheral sites. The solution would seem to be to sample early in the first brood or to in-

clude only the first 25–50% of the territories settled.

Concluding Remarks

I will conclude by briefly summarizing some earlier points to serve as suggestions or reminders for workers in both theoretical and applied avian ecology:

1. The world needs a universally applicable, reliable, simple, and ecologically meaningful method and index to quantify avian habitat, particularly the vegetative components of habitat. If we can establish broad-spectrum, reasonably predictive relationships between vegetation and community structure, the work of applied ecologists would be simplified and improved. Such a tool could be useful in pre- and postimpact assessment and in evaluating a major aspect of habitat quality for planning purposes. For example, the latter input could help determine which of two similar plots had the greater potential value in terms of avian resources (but, see Point 5 below for a warning about defining value).

2. Ecologists should consider going beyond reporting the status of communities only in terms of species richness, population density, or species diversity. These may or may not be accurate indices of the health or structure of a community. We should investigate their relationship to other community characteristics and indicators of "carrying capacity" such as existence energy, biomass, and guild composition. Only then will we know if the simpler characteristics are adequate compromises for situations in which ease and speed of data collection and analysis are critical.

3. If community research as discussed here leads to a sound understanding of vegetation-avian community relationships, there may be a temptation to manage vegetation to maximize avian diversity. I emphasize Balda's (1975) warning in this regard. In such a scheme there is the chance that rare or specialized species, with which we are often most concerned, could be managed out of existence since they have little effect on the diversity indices frequently used. I suggest managing instead for a "native diversity"—a richness or community organization typical for the region which includes species endemic to the particular locality and habitat.

4. Population density should be only a first approximation in assessing impact, habitat quality, or management success for a single species. A high population does not necessarily mean those individuals will be successful in terms of survival and reproduction, but only that many have been attracted to a particular site (Trautman 1960, Dow 1969). For example, to assess the impact of a highway on breeding birds in terms of community characteristics or of the population density of a single species is only part of the story. We should know if the birds that use the roadsides are productive, have normal survival rates, etc. In essence, ecologists should try to identify, assess, and manage ultimate as well as proximate factors of habitat selection. Good examples of this approach exist (Trautman 1960, Nettleship 1972, Gorman 1974, Higgins 1977).

5. We need to improve on results reported here for individuals and populations. We should determine the causes and the consequences of such patterns. Do changes affect foraging efficiency, food provisioning for the young, nest security, etc.? Burr and Jones (1968) noted that heights of robin (*Turdus migratorius*) and wood thrush (*Hylocichla mustelina*) nests were higher in parks than in other woods. While this suggests impact, we should know if reproductive output is

affected in such cases. With such evidence ornithologists can assess the long-term, subtle effects of vegetative alterations on bird populations.

6. Resource managers should consider the implications of large-scale single-species management plans on the total avian community. Since vegetation structure seems to be an important determinant in the ecology of many species, we should remember that alteration or maintenance of habitat to favor one species could make the habitat marginal for many others. This problem should be investigated to determine the extent of this effect, if indeed it exists. Siderits and Radtke (1977) and Gould (1977) discuss forest management schemes which offer two contrasting approaches to this concern.

7. It is important for two reasons to emphasize that vegetation structure affects the exploitation patterns and success of individuals. First, it helps us remember that population and community characteristics are consequences of activities, such as habitat selection, feeding, etc., of individuals and are not manifestations of strategies of these higher units. Second, ecologists must be able to show such effects at the individual level if we are to convince non-ecologists that habitat alteration is a serious threat to animal populations.

Finally, I have tried to indicate the ways in which my data were ambiguous and incomplete. I hope my vignettes and my suggestions will lead future researchers around some pitfalls. I assume they also will identify bird species and aspects of avian ecology that could be investigated fruitfully in south Texas and elsewhere.

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